

Chapter 4

Sitka Spruce (*Picea sitchensis* (Bong.) Carr)

Steve Lee, David Thompson, and Jon Kehlet Hansen

4.1 Introduction

Sitka spruce (*Picea sitchensis* (Bong.) Carr.) occurs naturally down the seaboard of the Pacific North West in Canada and USA. It is not a species of prime importance at a European level (1.2 million hectares), but is locally very important in certain North European countries with Atlantic coastlines.

Sitka is a main plantation species in Great Britain (700 thousand hectares) and Ireland (330k ha) and a minor species but of commercial concern, in Denmark (35k ha) and France (50k ha). It is increasingly being considered as a species for the future in the southern part of Sweden (currently 7k ha) and was considered an important exotic in Norway (50k ha) where it is often thought to be the most productive species available for west-coast sites. It is also planted in Iceland to a limited extent, often in preference to Norway spruce (*P. abies*).

Being an exotic is it a species for consideration under re-afforestation conditions and is rarely used to replace native species. Although perhaps minor at a European scale, there are still over 70 million Sitka spruce trees planted and over eight million cubic metres harvested each year, adding considerably to the local and sometimes

With contributions from:

Jean-Yves Gautry (FR), Bo Karlsson (SE), Bernt-Håvard Øyen (NO), Volker Schneck (DE) and Sven de Vries (NL)

S. Lee (✉)

Conifer Breeding, Forestry Commission Research Agency, EH 25 9SY Roslin, UK
e-mail: steve.lee@forestry.gsi.gov.uk

D. Thompson

Tree Improvement Section, Coillte Teoranta-The Irish Forestry Board,
County Wicklow, Ireland

J.K. Hansen

Danish Centre for Forest Landscape and Planning, University of Copenhagen,
1870 Frederiksberg, Denmark

national economies. The species is usually planted for construction timber although in Denmark it is increasingly being planted for bio-mass production. Small dimensioned material is readily used in the pulp and paper, and particle board industries. These details are expanded upon in the country-descriptions that follow.

This monograph will give the reader an indication of the importance of Sitka spruce across Europe, the extent of breeding within the region and plans for the future. The bibliography in particular can be used a source of further information for the reader who wishes to learn more.

4.2 Natural Distribution and Habitat

Sitka spruce trees are amongst the largest growing trees within the *Picea* genus. Under optimum conditions of site and climate they have been known to achieve 180–230 cm diameter at breast height (DBH; 1.3 m) and 70–75 m in height. They can also live for up to 500 years. Unlike most of the other spruce species it is a coastal rather than a continental species. It grows in a narrow coastal belt covering 3,000 km from Kodiak Island in Alaska, USA (58°N) through coastal British Columbia, Canada down to northern California, USA (41°N) with a disjointed population in Mendicino County, California (39°N; see Fig. 4.1). However, along this latitudinal distribution the climatic conditions are very similar with surprisingly little difference in temperature. Sitka spruce thrives mainly in the super humid fog belt along this western coast under conditions of mild winters and cool summers, without any summer drought. The main limiting factors for the species are high air humidity and available moisture. Sitka requires a minimum of 1,000 mm of rainfall per year in its natural environment. As a result it follows a strict maritime distribution and ranges from just a few kilometres inland around Oregon and Washington, up to 200 km inland adjacent to the river valleys systems in British Columbia. This distribution leads to one of the alternative common names for the species of “Tidewater Spruce”. As its native distribution implies, Sitka spruce is very tolerant of exposure and salt spray. The species grows mainly below 300 m in elevation but can be found from sea level up to 880 m in Oregon and Washington, and 1,000 m in Alaska.

Unlike many other conifer species Sitka spruce tends to maintain a rapid early height into mid-rotation ages. It grows on a wide range of soils but performs best on deep, moist, well drained (i.e. not waterlogged) soils such as alluvial soils, coarse textured soils, and soils with a thick organic layer with a pH of between 4.0 and 5.7. It does not do well on alkaline soils or deep peats. The species does tolerate poor, wet rocky habitats with acid soils. Throughout most of its natural range Sitka spruce grows in mixture with a number of species including western hemlock (*Tsuga heterophylla*) on drier soils, and western red cedar (*Thuja plicata*) on wetter soils, although it can also grow as large trees in pure stands. Outstandingly large individuals are found in the Olympic Peninsula of Washington and the Queen Charlotte Islands (QCI) off the coast of British Columbia. However, the tallest trees occur on the northern Oregon coast (45°N). For more detailed information regarding the ecology and management of Sitka spruce in its native range see Peterson et al. (1997).



Fig. 4.1 Natural distribution of Sitka spruce. 3,000 km from nearly 60°N in Alaska to around 40°N in California, but always close to the sea apart from river inlets

Sitka spruce forms natural hybrids with other spruce species within its natural range including *P. glauca* in Alaska and British Columbia to give a species known as *Picea* × *lutzii* (see Roche 1969 and Roche and Fowler 1975 for more details on the inter-crossing of *Picea* in British Columbia). Artificial hybrid combinations

with outstanding growth have also been made outside its native distribution including *P. sitchensis* × *P. omorica* and *P. sitchensis* × *P. glehnii* (Hoffman and Kleinschmit 1979). A comprehensive review of the genetics of Sitka spruce including its taxonomy, inter-species crossability, and morphological and phenological variation was made by Roche and Fowler (1975).

The first European to identify and describe the species growing in its native environment was Archibald Menzies in 1792. David Douglas was the first European to collect seed for transporting home in 1831. It is thought the first seeds were collected near the mouth of the Columbia River which separates Washington and Oregon (46°N). Resulting trees were planted in sponsors' gardens and arboreta in the UK and Ireland in the 1840s and 1850s. Some plants believed to have originated from this first collection are still growing in the Curraghmore Estate, County Waterford, Ireland (52°N), and Murthly and Scone Estates, Perthshire, Scotland (56°N). Initially, the species was not as popular as Douglas-fir or western red cedar but the potential for the species was being realised in Scotland where the first plantation was established in 1879. By the early 1920s the demand to replace timber harvested during the First World War (1914–1918) and the creation of the UK Forestry Commission (State Forestry Service) in 1919, led to a significant increase in planting of Sitka spruce. Its attributes of tolerance of exposure, and faster growth rate compared to native species or more demanding exotics such as Douglas fir made it particularly suitable for planting on the wet up-land sites that were being afforested at the time.

Sitka spruce wood is a light, soft and generally straight grained but strong and easily worked and it takes nails and screws well. The light colour and short fibres of the species make it unsurpassed in quality for pulp production. It has been used in the manufacture of a wide variety of items such as boxes, barrels, crates, for veneer and even musical instruments, including the sounding boards in pianos. Other wooden items include sailboat masts, spars, ladders, steps, studs, plates, rafters and joists, but it is not suitable for heavy construction purposes. The species is valued for its high strength to weight ratio and was used in the wooden frame of the first Wright brothers' airplane and in the frames of many aircraft used in the First World War. During the Second World War (1939–1945) it provided the wing spars of Mosquito aircraft for the British Royal Air Force. In the mid-1940s Sitka spruce was used by Howard Hughes to construct a huge wooden aircraft known as the "Spruce Goose". Today the nose cones of Trident nuclear missiles are made from Sitka spruce; a modern reflection of its high strength to weight ratio.

Sitka spruce is not a major commercial forestry species in Canada due to the local preference of Douglas fir; also the presence of the 'pine shoot' weevil (*Pissodes strobi*) that burrows into the apical shoots of Sitka spruce resulting in stunted trees with very poor stem form and low or no, commercial value. Fortunately this insect has not been reported in Europe. More recently a weevil-resistant breeding programme has been started in British Columbia with considerable success (King et al. 2004). There is currently no Sitka spruce breeding being carried out in the USA (Keith Jayawickrama 2010, Oregon University, personal communication).



Fig. 4.2 Sitka spruce origins demo line in south Scotland. Alaska on *left*; Washington on *right* (Source: Forestry Commission, Great Britain)

4.2.1 Distribution Outside Its Native Range

The first Sitka spruce introductions into Europe came from a limited part of its natural distribution which nevertheless showed the potential of the species when transposed to similar European maritime conditions. Most early imports of seed were from Washington and British Columbia and it was initially assumed (incorrectly) that there was little provenance variation. Early provenance trials were undertaken in Norway, Denmark, Germany and the UK but typically were based on commercial seed collections which covered only a small part of the species range. In addition, very few trials tested the same seed sources over a range of locations. The results of these early trials showed differences in survival were due mainly to differences in date of bud break and bud set in relation to local frost events.

Provenance selection for commercial production has always been a balance between growth rate, frost hardiness and branching habit. Southern sources tend to be the most vigorous if the climate allows (i.e. no late spring frosts; no early autumn frosts) as well as having fewer and finer branches than more northern sources. There is a very narrow range in the date of bud break between origins with perhaps a maximum of a 7–10 day difference between the earliest and latest flushing provenances; and northerly sources are not necessarily the latest to break bud. Date of bud set has a much wider range with Queen Charlotte Islands (QCI) sources setting bud in late August to mid-September and Washington sources setting bud in late September to mid October thus resulting in differences in damage caused by early autumn frosts (Cannell et al. 1985, Fig. 4.2).

Table 4.1 Summary of results of IUFRO Sitka spruce international provenance experiment after 6 years in the field

Country	Best sources	Comments
SE Australia	California and southern Oregon	California best
Belgium	British Columbia and QCI	Vancouver Island best
Bulgaria	Alaska for high moisture sites	
	Washington for sites in Norway spruce range	
Denmark	Land races of Washington and QCI	
	Washington imports also good	
France	Oregon, Washington and southern British Columbia good	S. Oregon good growth but much secondary growth
	Washington and S. Oregon best	
Germany	Washington and N. Oregon fastest growing	
	Southern British Columbia also good	
Ireland	Washington and Mid-Oregon	
Latvia	QCI and B.C.	Sitka spruce did not grow faster than Norway spruce. No end use.
Netherlands	Washington and N. Oregon	
New Zealand		No commercial value
Norway	Alaskan and northern British Columbia	
UK	QCI most stable	
Turkey	Washington and Oregon	
Yugoslavia	N. Oregon and S. Washington	

4.3 IUFRO Trials

As part of the IUFRO “Working Group on Provenance Research and Testing” a series of international provenance experiments was established for a range of species, including Sitka spruce. Material was collected from 84 specific locations along the species coastal range from Alaska to Northern California between 1968 and 1970. This material was distributed to 22 different countries for testing in the main IUFRO Sitka spruce provenance trial. While these trials consisted of large plots, not all trials included a common group of sources. As a result, a smaller subset of ten common provenances, known as the IUFRO Sitka Spruce International Ten Provenance Experiment, representing a broad sample of the entire geographic region occupied by the species was established by 13 countries. A summary of the early results of these trials is given in Table 4.1. More details can be found in Ying and McKnight (1993). Based on the results from the IUFRO trials and questionnaire returns from ‘Treebreedex’ partners who have or are currently planting Sitka spruce, a generalised map showing the likely deployment of Sitka spruce provenances across Europe is given in Fig. 4.3.

4.3.1 The Situation Now

Table 4.1 indicates that Sitka spruce has been tested in a large number of European countries but can only be considered a commercial species in Great Britain and Ireland,

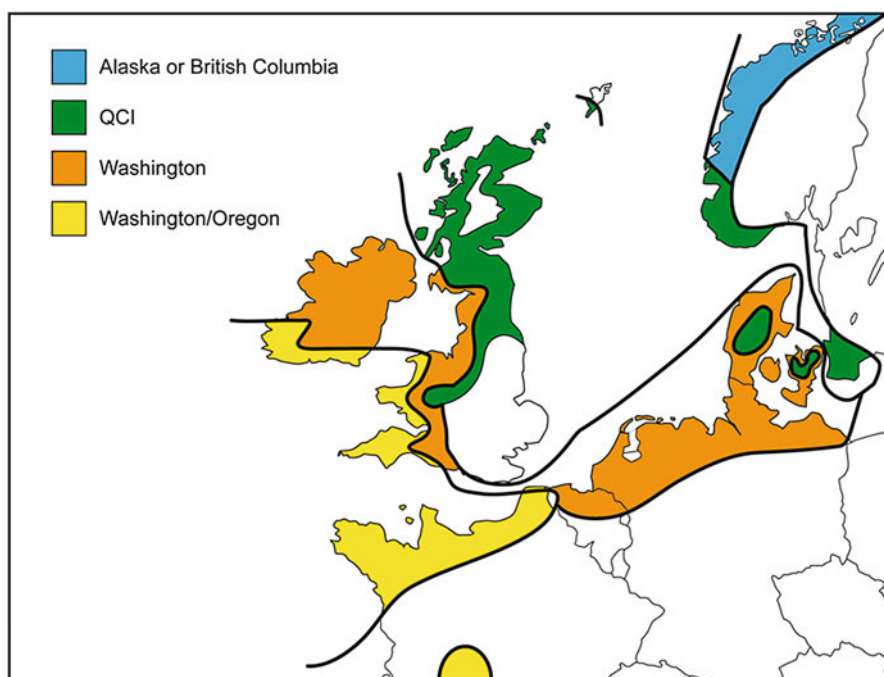


Fig. 4.3 Likely suitability of Sitka spruce origins in Europe. Based on questionnaire returns from TreeBreedEx partners that are planting or have planted Sitka spruce

although it has been important in Germany, Denmark and France in the past. Sweden remains a country where the popularity of Sitka spruce could increase in the future. Figures on total area planted, annual planting rates, percentage of national forest and annual volume harvested at a national level within Europe are all presented in Table 4.2.

4.4 Breeding

4.4.1 Introduction

From the data provided in Table 4.2, it is not surprising that the most advanced Sitka spruce breeding programmes are located in Great Britain and Ireland. Small, now dormant programmes have previously existed in France, Denmark and Germany. Depending on climate change predictions, a small Sitka spruce breeding programme may start in Sweden in the future. Otherwise Sitka spruce can not be considered a serious commercial species in Europe outside the western seaboard. It requires the cool, moist, oceanic environment common along the coast of northern and western coastlines of Europe similar to those it experiences in the Pacific North West (PNW). It does not tolerate a Mediterranean-type climate of very cold winters and hot dry

Table 4.2 Statistics on Sitka spruce planting rates and volume harvested in Europe

	Approx. total area of SS (ha)	% National forest area	Approx. mean annual planting SS (ha)	Approx. number SS trees planted each year	Approx. volume of SS harvested each year (m ³)
Great Britain	700,000	30	10,000 (peak of 18,000)	32,000,000	6,000,000
Ireland	330,000	52	7,500 (peak of 10,400)	30,000,000	1,500,000
Denmark	35,000	6	1,300	4,000,000	600,000
France	50,000	<1	250	300,000	No data
Germany	24,000	<1	ND	400,000 (exported)	55,000
Norway	50,000	<1	40	<100,000	40,000
Sweden	7,000	<1	Now 1,500	5,000,000	1,000–10,000
TOTAL approx.	1,200,000	<1–52	28,000	71,500,00	8,200,000

Note: *ND* no data available

summers. Rainfall requirements of around 1,000 mm or more are recommended although it can grow on sites with substantially less rainfall provided moisture deficits are low or roots have the opportunity of exploiting underground water sources.

A summary of breeding effort (Table 4.3), sources of improved material (Table 4.4), amount of field testing (Table 4.5, Fig. 4.4) and the components of deployed FRM (Table 4.6) are presented for each European country planting Sitka spruce. What follows below are details of country-specific breeding activities. In general the breeding objectives are for good quality construction timber and the characteristics under selection are survival, growth rate, stem straightness, fine branching quality and improved timber properties. Sitka spruce grown as a biomass crop is being considered seriously in Denmark and considered in Great Britain when there is no alternative species of higher calorific value.

4.4.1.1 Great Britain

Background

Soon after its discovery by Europeans in 1831 Sitka spruce was introduced to Great Britain and has been an important reforestation species for the last 100 years. By the time the British Forestry Commission was established in 1919, experience from sample trees planted in arboreta and on large estates had shown the species to be fast-growing, hardy in exposed conditions and capable of growing on site types which at the time were mainly planted with Norway spruce (*P. abies* (L.) Karst.) or occasionally Scots pine (*Pinus sylvestris*) of western-coast provenance. The superior growth of Sitka spruce ultimately led to an increase in its popularity through the 1930s and beyond as the forest estate expanded under the government policy of afforestation pertaining at the time.

Sitka spruce is now the most widely planted conifer in Great Britain, accounting for nearly 700,000 ha of forest or 30 % of the total forest estate (Forestry Commission 2008). The species is well suited to the areas of high rainfall and lower quality soils that predominate in the north and west of Britain (Fig. 4.5). It is planted from Cornwall in south-west England (51°N), through Wales and north-western England, across north-eastern England and southern Scotland and up into the Scottish Highlands (58°N; see Figs. 4.5 and 4.6).

The annual growth in Britain ranges from 12 to 26 m³/ha/year. Commercial rotation lengths are typically 50 years down to 35 years if wind-throw, due to shallow rooting on wet soils, is a limiting factor.

Breeding

The main breeding objective in Britain is to increase the end-of-rotation value of construction grade timber relative to that achieved using unimproved seed imported from the Pacific Northwest. Trees are selected which combine good growth rate,

Table 4.3 Breeding effort by European country

	Main origin of breeding programme	Number of candidate trees selected	Size of breeding population	Degree of activity in the breeding programme
Great Britain	QCI	1,800	360	Active. Main commercial species. Tested seed orchards and large VP programme. Plans to advance into second generation; clonal testing; development of SE/ cryo; use of DNA-markers to assist breeding
Ireland	Washington	750	36–86	Active. Main commercial species. Improved material available through VP involving SE and cryo programmes. Aim to maximise gains from first generation. Two recently planted seed orchards
Denmark	Washington + QCI	Approx. 100	Approx. 1,000	Not active today. 3 'series' created in past; 2 × Washington; 1 × QCI. Productive seed orchards exist
France	Washington + Oregon + California	Approx. 200	Nothing organised	Not active today.
Germany	SW British Columbia + Washington	ND	Nothing organised	Some clonal selection and testing in 1990s Not active today.
Norway	Alaskan + some QCI	ND	ND	Some plus tree selection in past to trial hybridisation with other spruce species Not active today.
Sweden	QCI	ND	65	Very low priority. Some plus tree selection in past. One seed orchard Increasing Activity Possible species for the future as climate warms in the southern tip of the country.

Note: *ND* no data available

Table 4.4 Sources of improved material – seed orchards and VP, and predicted gains

	Number of seed orchards	Area	Predicted gains from seed orchards	Predicted gains from other sources
Great Britain	8	20 ha	Gains range from: DIAM 15–22 % STR 5–22 % DEN 0 to –12 % VOL: 21 to 29 % (mean 25 %) at rotation SAWLOGS: approx. 20 % increase in quality logs	VP of tested full-sibling family forestry: DIAM: approx. 20 % STR: approx. 20 % DEN: no significant reduction
Ireland	2	9 ha	Young seed orchard; not yet productive; predicted as: HT: 15–20 % STR: 7 % DEN: no significant reduction	SAWLOGS: Approx. 40 % increase in quality logs VP of (untested) full-sibling families from tested parents: HT: 20–25 % STR: 10 % DEN: no significant reduction
Denmark	4	15	FP.243: DIAM 3 %; DEN –1.5 %; STR approx. 15 %; lower spiral grain FP.250: DIAM 6 %; DEN –0.5 %; STR approx. 11 % FP.625 (WSS): VOL 30 %; STR 5 %; Forks 2.5 %; DEN no change; Leader loss 7 % less FP.256: DIAM 8 %; STR 7 %; DEN no change; later bud burst FP.611: Resistance to green spruce aphid	None
France	–	–		
Germany	1	1	No data on gains.	
Norway	3	10	Seed occasionally harvested; used internally or exported	
Sweden	1		Should be a small gain due to phenotypic selection Young seed orchard; not yet productive	

Table 4.5 Statistics on amount of field-testing

	Population or provenance trials	Progeny tests	Clonal tests	Clonal archives
Great Britain	53≈50 ha	392≈300 ha	30≈20 ha	2≈20 ha
Ireland	13≈26 ha	41≈34 ha	18≈15 ha	3≈15 ha
Denmark	14≈10 ha	19≈8 ha	19≈6 ha	
France	18 (9 still active) ≈19 ha	4≈6 ha	4≈3 ha	5≈10 ha
Germany	3≈2 ha	2 (1 still active) ≈0.5 ha	–	–
Norway	7≈6 ha	2≈2 ha	–	–
Sweden	–	8≈8 ha	1≈0.5 ha	2≈0.5 ha

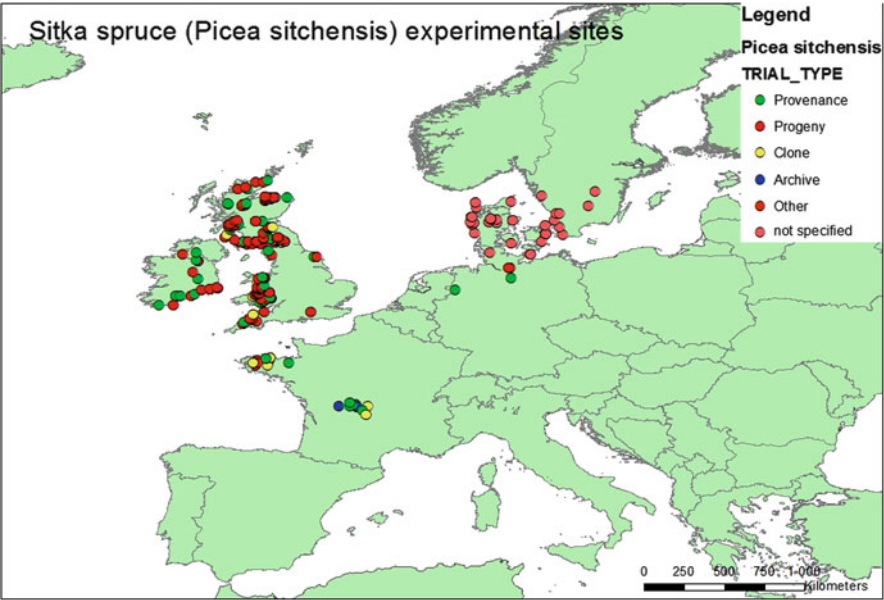


Fig. 4.4 Experimental genetic field trials across Europe (source: Treebreedex genetic resources database)

with improved stem straightness and branching qualities, and better wood stiffness. Wood stiffness is a complex trait involving wood density, microfibril angle (MFA) and other internal characteristics such as proportion of compression wood. Under current practice, only wood density is screened as a surrogate for wood stiffness although new screening methods employing acoustic tools as an indirect measure of MFA on standing trees are now being introduced (Mochan et al. 2009).

The breeding of Sitka spruce in Britain followed classical breeding techniques *viz* selection of the best origin, selection of plus trees from stands in forests, followed by testing of the selected plus trees usually by a series of comparative half-sibling

Table 4.6 Proportion of planting stock from alternative sources

Country	Seed orchard	Vegetative propagation	Seed stands	Direct import
Great Britain	70 %	20 %	<10 %	0 %
Ireland	45 % ^a	10 %	45 %	0 %
Denmark	90 %		<5 %	<5 %
France	ND	ND	ND	ND
Germany	ND	ND	ND	ND
Norway	<5 %		95	
Sweden	40 % ^b	60 % ^b	0 %	0 %
Netherlands	ND ^c		ND ^c	

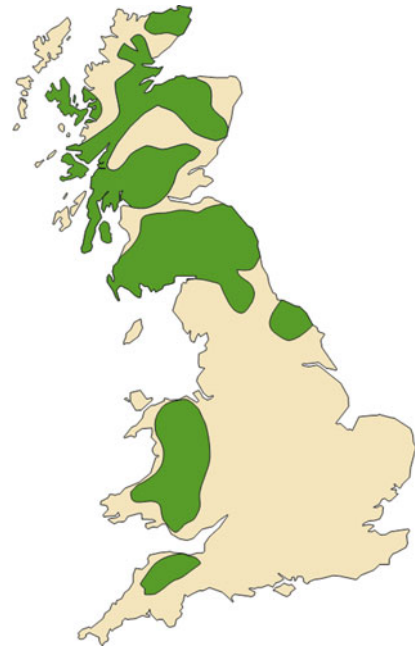
Note: *ND* no data available

^aEstimated as proportion imported from Danish seed orchard of Washington origin

^bEstimated

^c*ND* no data but all material imported from Denmark

Fig. 4.5 Main Sitka spruce planting areas in Britain. Sitka spruce is predominately planted in the areas of high rainfall in the west and northern Britain (Source: Forestry Commission)



progeny tests, subsequent measurement of trials and then re-selection of the best parent plus trees to form breeding and production populations (Fletcher and Faulkner 1972; Lee 2001; Lee and Connolly 2010). Samuel et al. (2007) summarised the processes involved in identifying provenances best suited for planting in Britain from the 53 trials planted (Table 4.5). The general conclusion was that material from the QCI (54°N) was most suitable for the greater part of Britain, although in the milder areas of southwest England and Wales, Washington sources (48°N) or occasionally Oregon material (45°N) were well adapted (see Fig. 4.7).



Fig. 4.6 Clear-felling good quality mature Sitka spruce in Northern England (Source: Forestry Commission, Great Britain)

Plus tree selection in Britain commenced during the early 1960s (Fletcher and Faulkner 1972) and continued into the early 1980s. Over 1,800 candidate trees of predominately QCI origin were selected (Table 4.3). Nearly 400 progeny tests were established with open-pollinated seeds (Table 4.5). Each candidate plus tree was evaluated in replicated trials established on an average of three sites, and compared against standard controls of unimproved imported QCI and Washington origin (Lee 2001; Lee and Connolly 2010). Test design varied in the early years with 8-tree row plots and 5 complete replications being the most common.

The trials were measured regularly for height followed by stem diameter at breast height (DBH; 1.3 m), stem straightness and latterly wood density. The best 360 plus trees have been re-selected based on a multi-trait index combining progeny data for

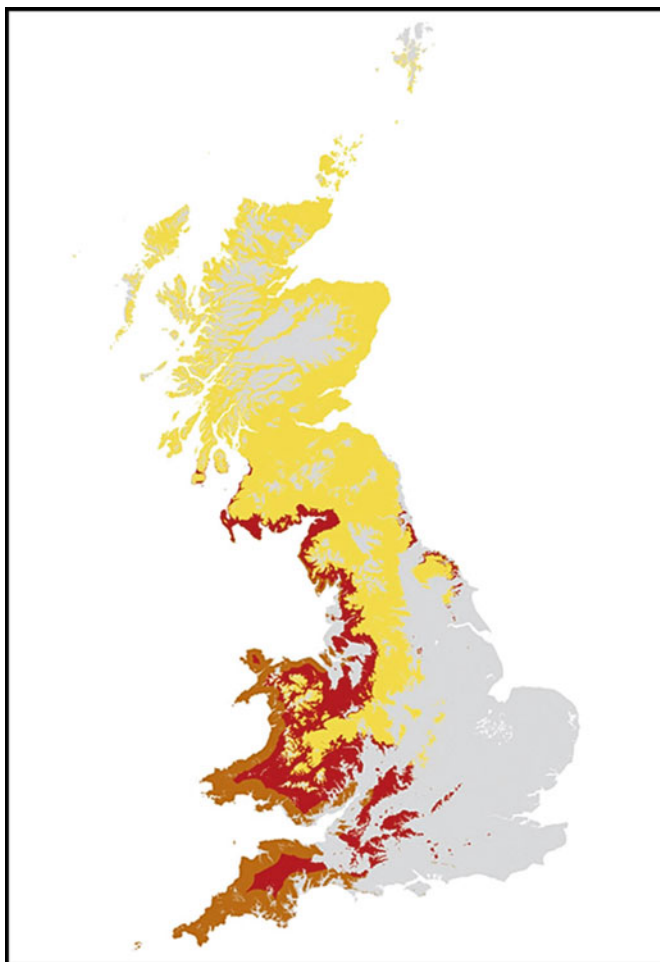


Fig. 4.7 Origin suitability within Britain. The bulk of Britain is best suited to QCI origin (yellow) but more westerly or southern sites may grow seed adapted to Washington State (red) or even Oregon (brown). Grey=not suitable area (Source: FC Bulletin 127, Samuel et al. (2007))

15-year stem diameter, straightness and wood density to form the breeding population. In the second generation, the programme expects to stratify the breeding population into six sub-lines of equal mean genetic value and to apply positive assortative mating within each sub-line (Lee 2001). An equal number of unrelated individuals from each sub-line will be brought together to mate in the next generation of seed orchards.

There is just one improved population for the whole of Britain known as the General Breeding Population (GBP). Plans for 'northern' and 'southern' breeding populations were abandoned on grounds of cost and predictions of better gains from the highly-selected GBP on both the more testing site in northern Scotland and warmer southern sites. Informal agreements are in place to co-operate with Ireland if demand for southern origin stock increases in the future or genetic gain advantages become apparent.



Fig. 4.8 Controlled pollination of Sitka spruce in a clonal archive in Britain (Source: Forestry Commission, Great Britain)

There is currently no resistance breeding in either Britain or Ireland. Although planted trees are often damaged by insects such as *Elatobium abietum* (green spruce aphid), *Hylobius abietis* (pine weevil) and *Dendroctonus micans* (great spruce bark beetle) and root-rotting fungi such *Heterobasidion annosum*, it is thought to be more economic to address these problems through silviculture and stand management. As previously mentioned, the potentially highly damaging insect ‘pine shoot’ weevil (*Pissodes strobi*), which causes massive problems for Sitka spruce in Canada is currently absent from Europe.

Improved planting stock has been available from the Sitka spruce breeding programme since the early 1990s. It can be derived either from seedlings raised from seed collected in progeny-tested clonal seed orchards, or as rooted cuttings derived from donor plants originating from controlled pollinations between re-selected plus trees growing in clonal archives (Table 4.6). The controlled pollination of selected seed parents uses a polymix of 20 or so unrelated pollens, again from selected trees. Predictions of genetic gain have been impressive (Table 4.4), up to around 20 % for both stem diameter and stem straightness with minimal loss in wood density. More recently, these half-sibling family mixtures have given way to full-sibling families offering further gains due to within family uniformity (Lee 2006). Sawmill studies involving trees from some of the earlier half-sib progeny tests have suggested end-of-rotation gains for volume of around 21–29 % (mean around 25 %) relative to unimproved QCI stock (Lee and Matthews 2004), and an increase of high-end value sawlogs of up to 130 % (Mochan et al. 2008, Fig. 4.8).



Fig. 4.9 Semi-mature full-sibling progeny trial in northern England (Source: Forestry Commission, Great Britain)

Improved material is in high-demand and is now entirely satisfied from home-produced improved sources. Around 32 million Sitka spruce trees are planted annually in GB (Table 4.2); 84 % (26 million trees) are from improved sources (20 million from seed orchards; 6 million from vegetative propagation). The balances (6 million trees) come from registered seed stands. There is no need to return to the Pacific North West (PNW) for seed (Forestry Commission 2010, Fig. 4.9).

Clonal forestry is not being practised in Britain although around 30 clonal tests have been planted over the years (Table 4.5) to investigate the extra gain which could be achieved by selected outstanding genotypes within a family (Mboyi and Lee 1999). Research continues to develop somatic embryogenesis

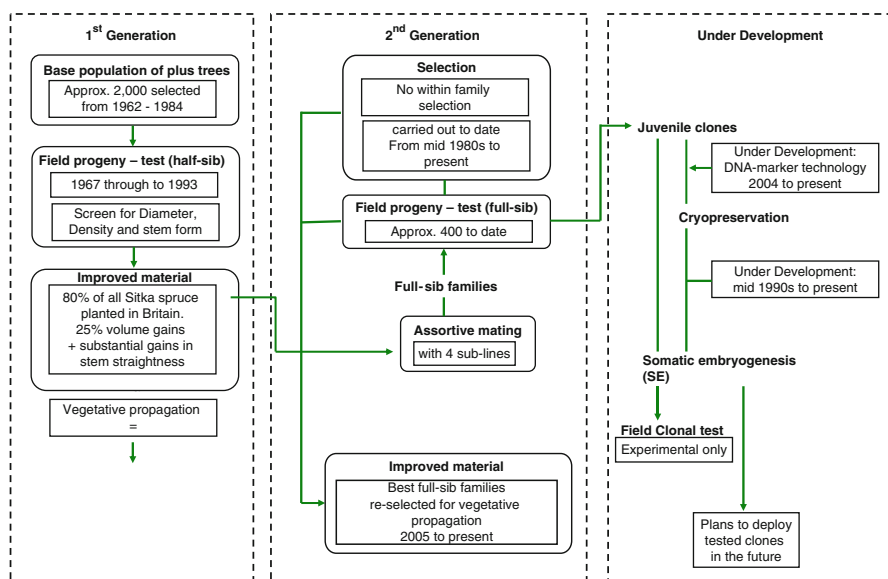


Fig. 4.10 Flow chart showing the progression of Sitka spruce breeding in Britain

(SE) and cryopreservation protocols for Sitka spruce. These are the technologies required to exploit the potential high gains which will come with clonal forestry. Breeders hope to identify rare individuals with high growth rate, good stem straightness, fine branching and above average wood stiffness. SE is a tissue culture technique for mass production of selected individuals, and cryopreservation prevents an ageing of the material whilst testing takes place in the field (Lee et al. 2004).

Britain is collaborating with Canada (<http://www.genomebc.ca/>) and others in Europe (www.noveltree.eu and www.procogen.eu) to identify DNA-markers associated with a range of economically important traits, including wood density. There has been a large investment in Marker Aided Selection (MAS), with an initial objective to identify a suite of DNA-based markers which could be used in the laboratory as surrogates for direct field selection of wood density and stiffness. Three large clonal trials were planted in 2004 on climatically contrasting sites across Britain. Each trial contains the same material; 1,500 clones from each of three full-sib families as well as the usual QCI control. It is hoped that the tests will enable the identification of quantitative trait loci (QTL) contributing to wood density, stem and branch quality (Lee et al. 2006). If successful, the SE/cryo techniques mentioned above will be essential for the rapid deployment of clones identified in the MAS programme.

A flow chart showing the progression of the Sitka spruce breeding programme in Britain is given in Fig. 4.10.

4.4.1.2 Ireland

Background

Sitka spruce was also introduced to Ireland in the early 1830s where it was planted mainly as single specimen trees in private estates and arboreta. The first plantations were established in the 1870s and 1880s, but it was in the 1920s when it was first planted as a commercial species as part of the state reforestation programme.

As the western-most European country, the mild (average winter temperature of 4 °C and summer temperature of 15 °C) and wet (ranging from 2,000 mm in the west to 750 mm in the east) climate of Ireland is well suited to the planting of Sitka spruce. The late occurrence of autumn frosts means that more southern origins of Sitka spruce from the coastlines of Washington and Oregon outgrow the QCI favoured in Britain. Growth rates tend to be high ranging from 14 to 24 m³/ha/year or more with an average around 18 m³/ha/year. Rotation lengths are approximately 35–40 years (Fig. 4.11).

Sitka spruce is now the main commercial plantation species in the Republic of Ireland (Table 4.2). There are nearly 330,000 ha representing more than 50 % of the total forest estate planted between approx. 51–55°N. Planting rates in the recent past (10 years ago) were very high and peaked around 10,400 ha/year. This has fallen more recently to around 4,500 ha/year as a result of an overall reduced national planting programme, which still represents some of the highest annual planting rates in Europe. The age of Sitka spruce plantations in Ireland are younger than Great Britain so although the planting rates are very high, the annual harvested volume is currently lower, at around 1.9–2.6 million cubic metres per year. This is set to increase as more plantations mature. Based on an assumed volume/ha at clearfell of 400 m³, an annual harvest peak of 10 million m³ seems quite likely. The larger dimensioned harvested timber goes primarily as sawlogs for the construction industry, while the smaller dimensions are used for pulp, pallet wood, firewood and residues for wood-fuel. The panel board industries (chipboard, Medium Density Fibreboard; MDF, and Orientated Strand Board; OSB) are also of increasing importance. For a general reference on Sitka spruce and its planting in Ireland see Joyce and O'Carroll (2002).

Breeding

Results from 13 provenance trials (Table 4.5) have shown that material from Washington is the most productive for Irish climatic conditions, with Oregon material being planted along the south coast (Fig. 4.2). Descriptions of where Washington and Oregon sources should be planted in Ireland are given in Thompson et al. (2005) and Thompson (2007). The performance of various origins in the Irish IUFRO trials can be found in a report by Thompson and Pfeifer (1995).



Fig. 4.11 Sitka spruce plus tree in a registered seed stand in Ireland (Source: Coillte Teoranta, Ireland)

The Sitka spruce breeding programme in Ireland is the second largest in Europe. All of Ireland is considered to be one breeding zone with no significant Genotype \times Environment ($G \times E$) interactions. The original objective was to select 1,000 plus trees in above average Sitka spruce plantations, but only 747 were selected of which 550 were progeny tested across 41 trials (Tables 4.3 and 4.5). Test design was typically 40 trees per site, 3 or 4 sites using randomised complete blocks. About 86 parents were then re-selected based on increased productivity and improved stem form following data collected in the half-sibling trials. Further re-selection of parents on the basis of no significant loss in wood density reduced the number to 36 which form the basis of the current breeding population. In most cases records exist

on the parent origin and it is possible to avoid crossing individuals which may have been selected in the same seed lot and so might be related. Full-sib crosses between the re-selected parents are now in test, as are clones randomly selected from within some of these full-sib crosses.

Due to irregular flowering, the seed orchard option has not been pursued historically, in Ireland. There have been two recent orchard plantings of Irish-selected material, but these are not yet productive. The main source of improved material has been rooted cuttings. Full-sib crosses of the best parents (currently under test) are used to establish embryogenic cell lines which are both cryopreserved and used to produce stock plant hedges. Cuttings are harvested from the hedges, and rooted in nurseries to produce improved rooted cuttings for field planting. Genetic gains from this source are estimated to be 15 to 20 % increase in height, 7 % increase in stem form and no significant reduction in wood density (Table 4.4). The rooted cuttings material (approx. 3 million trees per year; 10 % of requirement) does not currently satisfy annual planting demand. The balance of planting stock is 50 % from a Danish seed orchard of Washington origin, and 50 % from home collected seed stands. Seed is no longer imported from the USA.

An interesting development of the breeding programme in the early 1980s was a clonal programme following the ideas of Kleinschmit (1974). This involved selecting 'superior' phenotypes in nursery beds, propagating them by cuttings and then re-selecting based on nursery trials to identify clones for field testing after 2–3 cycles of selection. Fast growing individuals were identified, but 'serial propagation' was not able to delay maturation sufficiently to allow continued efficient propagation of this material and the programme was eventually abandoned.

4.4.1.3 Denmark

Background

Sitka spruce was introduced to Denmark in the early 1860s and became more regularly planted in reforestation programmes at the end of the nineteenth century. Sitka spruce now makes up 34,000 ha or 6.5 % of the total forest estate in Denmark (Table 4.2; Nord-Larsen et al. 2008). It is planted mainly on sandy soils and moraines due to its tolerance of sea-salt in the area of Jutland (56°N) but only where the sand layer is thin (less than one metre) and the trees are able to reach a water supply in a clayey- or sandy moraine substrate (Fig. 4.12).

Sitka spruce plantations suffer regular attacks from the green spruce aphid (*Elatobium abietinum*) and various beetles, in particular *Dendroctonus micans* which can be very harmful in dry summers. The site-type choice contrasts with the wet peaty and gley soils favoured in Ireland and Great Britain. Mean annual precipitation of Sitka sites in Denmark varies from approximately 500–900 mm per year but it is only planted on sites which have permanently damper soils beneath the surface. This again contrasts with the much higher rainfall (700–2,000 mm) in Ireland and Great Britain. Day degrees >5 °C are typically about

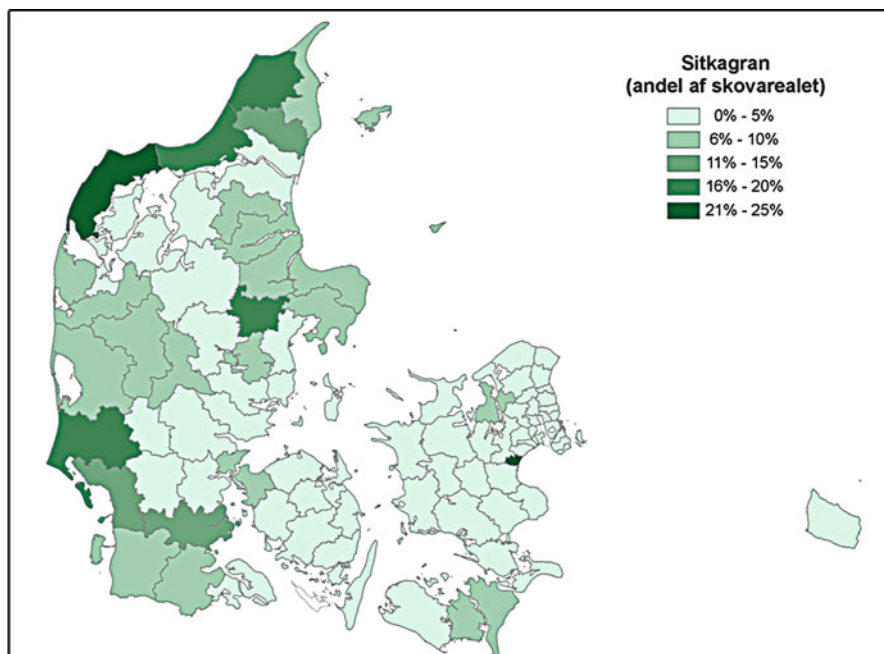


Fig. 4.12 Planting Sitka spruce in Denmark. Most areas have 5 % or less coverage but this rises to over 20 % along the West of the country, next to the North Sea

2,000 (estimated from the local climate predictor of FAO (Grieser et al. 2006)) which is common in Ireland, but only true of the extreme SW England within Great Britain. In Scotland the equivalent AT5 figure can often be around 1,000–1,500 (Fig. 4.13).

Planting density in Denmark is 2,800 trees per ha which is similar to planting densities in Ireland and Great Britain.

Breeding

Fourteen provenance trials were planted in Denmark (Table 4.5) which identified the best sources as being Washington in western Denmark and QCI in eastern Denmark (Fig. 4.2). The current Sitka spruce breeding populations are based on first or second generation material from these areas. The current breeding programme, although at a first generation stage, is quite advanced and has benefitted from considerable past investment. Clonal seed orchards have been established (Table 4.4) and clones have been tested in either progeny or clonal field tests followed by further re-selections for tested clonal seed orchards (Table 4.5). Denmark is now self-sufficient in improved material (Table 4.6) and sells surplus material to other European countries such as Ireland.



Fig. 4.13 Young Sitka spruce growing on sand dunes in Denmark (Source: University of Copenhagen, Denmark)

All breeding material is based on Danish landraces. The breeding programme is along the lines of nucleus breeding with one main population and three series which have been developed for the following site types:

1. Fertile sites with a small risk of late frost in spring and early frost in the autumn;
2. Poor sites with medium risk of frost;
3. Less fertile sites with risk of severe frost (Roulund 1990).

The first series is based on trees thought to be of Washington origin. In this breeding population selections are mainly aiming to improve wood density, stem straightness, spiral grain (reduction in juvenile wood), volume and frost tolerance (Roulund 1990 with modifications). This series encompasses approximately 600 trees represented in clonal field orchards, clonal archives and clonal field tests. Offspring from clonal seed orchards in this series are suitable for sites that are less exposed to frost, i.e. mainly sites in the western part of the country as well as sites near the west coast of Jutland. It is recommended for more fertile sites where the fast growth is anticipated to decrease wood density, influence stem straightness negatively and increase the proportion of juvenile wood with spiral grain. These drawbacks are counteracted by selection of genetic material with improved wood density, stem straightness and reduced spiral grain in the juvenile wood.

The second series is based on trees thought to be of QCI origin aimed at sites with higher risk of late spring frost and early autumn frost. Selections within this population are targeting volume production; stem form and survival at more harsh sites, i.e. frost tolerance (Roulund 1990 with modifications). Offspring from clonal seed orchards in this breeding population is recommended mainly for sites in the inner parts of Jutland and eastern Denmark with higher risk of late frost in spring and early frost in the autumn. This nucleus includes around 350 trees represented in clonal seed orchards and as clones in clonal field tests and clone archives.

A third series was established in the 1990s, targeting sites extremely prone to late spring frost and early autumn frost and includes hybrids between Sitka spruce, white spruce (*P. glauca*) and Serbian spruce (*P. omorika*; Roulund 1990).

As in Ireland and Great Britain there is a development programme into SE and cryo-preservation. This has not yet been developed into an operational level. Unlike Ireland and Great Britain, there is currently no vegetative propagation programme in Denmark.

Problems with insect and disease attack are anticipated to increase in frequency with climate warming and for this reason the demand for Sitka spruce seed in Denmark is anticipated to decrease. Consequently no further funding is available to continue the breeding programme.

Biomass Production

Denmark currently varies from the other major Sitka-growing countries in its interest in growing the species for biomass production. Preliminary results from field trials with a number of tree species in Denmark (age 43 years) have indicated that Sitka spruce generally has the highest biomass production on the sites thought to be available (Nord-Larsen et al. 2008). Additionally, Sitka spruce demonstrated good biomass breeding potential with one clone having 100 % higher dry matter production relative to a standard in a 23-year-old trial (Costa e Silva et al. 1994). This has raised an interest to screen the existing breeding program for Sitka spruce in Denmark for high biomass production. One other country currently interested in the high productivity of Sitka spruce is Lithuanian. There is just one provenance trial in that country at the moment but the over 500 m³/ha production over just 33 years gives an indication of its potential for wood fuel there (Darius Danusevicius, Lithuanian Forest Research Institute, personal communication). Extreme winter temperatures of −25 °C are the restriction to further planting, but if the climate warms there may be a potential for the species on carefully selected sites.

4.4.1.4 France

Background

Sitka spruce was first introduced in France in the early 1900s and was planted mainly as a specimen tree in parks and arboreta. Only after the Second World War



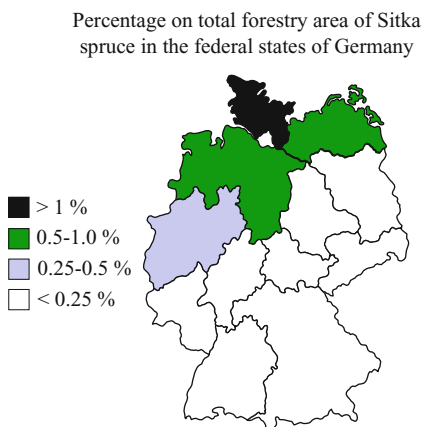
Fig. 4.14 Mature Sitka spruce growing in Brittany, France (Source: FCBA, France)

did interest develop in this species for reforestation purposes. It is a minor species in France representing less than 1 % of the national forest estate. It has been planted in the north-western part of the country (Normandy and Brittany; approx. 48°N) and west Massif Central (approx. 45°N), representing the most southerly commercial planting of the species in Europe (Fig. 4.14).

Breeding

Eighteen provenance trials (Table 4.5) have shown that Washington sources are best for the north and north-eastern parts of France while Oregon material is best for

Fig. 4.15 Main Sitka spruce growing areas in Germany. Sitka is clearly a minor species. It never exceeds 1 % of the land cover and is absent from most regions



north-western and central locations (Fig. 4.2). There is no active breeding programme today, although FCBA (formerly AFOCEL) did conduct a programme in the 1980s and 1990s involving the selection of around 200 plus trees (Table 4.3). The programme was centred on more southerly origins, mainly Washington and Oregon but also some from California. Today there is one selected seed stand but no seed orchards (Table 4.4), although there has been a programme of testing provenances, progenies and clones. The species is still planted to a limited extent (Table 4.2) with seed being imported from Washington or Oregon. Material from Danish seed orchards, and progenies from Ireland, Scotland and French selections have been established previously in field trials.

4.4.1.5 Germany

Background

The first Sitka spruce trees planted in Germany were soon after its discovery in 1831; the first plantations were established in the 1880s and it has been used as a reforestation species for the last 130 years.

Although today Sitka spruce is a minor species in Germany, it was more commonly planted 30–50 years ago. At around 23,000 ha it represents less than 1 % of the total forest estate (Table 4.2), and is restricted to the areas of higher rainfall and humidity along the coasts of the North and Baltic Seas (approx. 54°N), and to a more limited extent in northern mountainous areas with high rainfall (Fig. 4.15).

The species is grown over a 60–80-year rotation and currently approximately 50,000 m³ are harvested annually for the construction timber market. As in Ireland and Denmark there has been an increase in attacks by insect pests, perhaps due to conditions of drought stress and localised wind-throw problems of this shallow-rooting species have added to its recent demise.

Breeding

In Germany provenance recommendations, based on early provenance tests from the late 1920s and the more recent IUFRO trials, are for origins from north-western Washington and south-western British Columbia mainland. There has never been an active breeding programme although one (untested) 16-clone seed orchard does exist of plus trees selected in stands on the coast of the Baltic Sea near to Rostock.

The main area of interest has been hybridizing Sitka spruce with other *Picea* (Geburek and Krusche 1985). Crossings between Sitka spruce and Serbian spruce were done at the end of the 1950s and the beginning of the 1960s. In 1961, field trials were established to estimate the performance of *P. omorica* × *P. sitchensis* hybrids in comparison with the parent species. With the exception of one site the results show a clear superiority of the hybrid families in comparison with the offspring of both parent species. Pooled over all trials, the mean heights of the hybrids at 4-years old amounted to about +60 % using the best eight trees per plot. This superior growth tended to decrease with age and was around +20 % by 15-years.

Future planting stock will likely be sourced from selected stands growing in Germany, from the single German seed orchard (Table 4.4), and to a lesser extent importation from North America or an appropriate Danish seed orchard.

4.4.1.6 Netherlands

Background

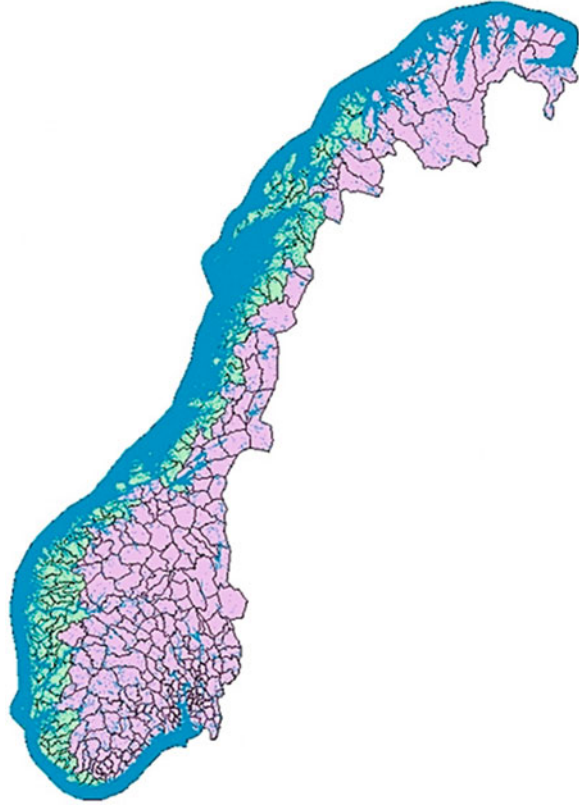
Sitka spruce is of minor importance in the Netherlands (2,075 ha) making up less than 1 % of the total forested area. In the 1970s Norway spruce was often replaced by Sitka spruce during reforestation activities, especially in the north of the country but this activity seems to have reduced somewhat. Rotation lengths are similar to Norway (60–80 years) as are uses of the timber which includes construction, timber frames and windows.

Breeding

Apart from important economic traits such as growth rate and form, time of flushing and survival were very important in determining whether a provenance was well adapted to the climate of the Netherlands. IUFRO trials suggest that Washington or Oregon sources are best adapted. As there are no seed stands of Sitka spruce in the Netherlands all seed is currently imported from abroad – mainly Danish seed stands and the Danish seed orchard FP 611. See Kranenborg and de Vries (2003) for a review.

Breeding has not progressed beyond the stage of selecting the best origin.

Fig. 4.16 Potential of Sitka spruce in Norway. *Light green* areas represent potential planting sites



4.4.1.7 Norway

Background

The first planting of Sitka spruce in Norway was about 1874. Although some planting was carried out in the 1920s and 1930s it was in the 1950s that interest in Sitka as a reforestation species for the west-coast of Norway (58–69°N) really developed. This represents the most northerly planting of the species in mainland Europe pushing through into the Arctic Circle (Fig. 4.16).

There are now 50,000 ha of Sitka spruce in Norway but only 40 ha are currently planted each year (Table 4.2). Despite its current lack of popularity on grounds of its 'exotic' status, it is recognised as being a productive species for the sites planted. Rotation length is around 80 years when the standing volume can be over 1,000 m³ per ha. Around 40,000 m³ are currently harvested, but this will rise as the 1950s plantations are felled in the 2030s. The wood is used for pulpwood and construction timber with most of the annual cut being exported to Germany (Fig. 4.17).



Fig. 4.17 Sitka spruce growing on the coast in northern Norway (Source: Norwegian Forest and Landscape Institute, Norway)

Breeding

The most suitable origin of Sitka spruce for west-Norway north of Bergen is SE Alaska (Petersburg, Ketchikan and Kruzow). Most of the material originates from Seward, Alaska. Areas to the south of Bergen (SW Norway) could be planted with trees of QCI origin. Plus tree selection has been carried out in west and north Norway leading to the creation of seed orchards for these areas (Table 4.4). One further orchard has been established on behalf of Iceland where the species is predicted to perform better than Norway spruce under future climate change predictions. No other breeding work has been carried out. Bauger (1978) gives a general summary of the variation of Sitka spruce provenances growth in older plantations in West and North Norway, and Øyen (2005) details likely yield in stands of Sitka spruce.

4.4.1.8 Sweden

Background

Sitka spruce was first planted in Sweden around 1900 and has been planted sporadically since the 1940s, however, it is only in the last 20 years, and particularly in the last 5–10 years, has there been significant interest in it as a reforestation species.

Although currently a minor species in Sweden, more interest is now being taken of Sitka spruce for the moist, good fertility soils of south-western Sweden (59°N). The total amount of Sitka in Sweden is currently estimated around 7,000 ha (Table 4.2) of which 3,000 have been planted over the last 2 years.

Breeding

Seed origins of Sitka spruce from QCI are thought to be most suited for growing in southern Sweden. There is one registered seed stand, a small orchard planted in 2005 based around a 65 plus tree selection and there are plans for a further seed orchard in the near future. The plus trees are currently being progeny tested (Table 4.5). It is expected that any new trials will be of a clonal/progeny testing types (as per the Norway spruce programme in Sweden; Karlsson, personal communication).

The breeding programme is in its infancy and much will depend on how the climate appears to change. If it becomes warmer and remains moist in SW Sweden, there is expected to be an increased demand for Sitka although it is not a preferred species under the Forest Certification Scheme due to its exotic status (as in Norway) (Karlsson 1995, 2007). If future resources are directed towards Sitka spruce, then progress could be rapid as techniques developed for Norway spruce could be brought into play including efficient trial design, the use of rooted cuttings (VP) for deployment of superior families, and possibly the use of somatic embryogenesis and cryo-preservation to deploy selected clones.

4.5 Quantitative Data

Trends in heritability, age: age correlations and between trait correlations are drawn together from across the European breeding programmes and are expanded upon in Tables 4.7 and 4.8.

4.5.1 Heritability of Traits

Growth: Individual tree narrow and broad sense heritabilities in field trials with Sitka spruce are mostly low to moderate. No clear tendencies are found as regard the development in heritability with age (Gill 1987; Johnstone and Samuel 1978; Jensen et al. 1996; Lee et al. 2002a).

Wood density: The narrow and broad sense heritabilities for this trait are generally moderate to high, but tend to decrease with age (Lee et al. 2002b). Costa e Silva et al. (1994, 1998) found highly significant differences between clones.

Table 4.7 Examples of broad-sense and narrow-sense heritability for various quantitative and qualitative traits estimated from a wide range of Sitka spruce progeny and clonal trials across Europe

Trait	Age	Broad sense heritability (H^2)	Narrow sense heritability (h^2)	H^2 (clone mean)	h^2 (family mean)	Reference	Notes
Flushing	5			0.87–0.88		Nielsen and Roulund (1996)	Two clonal field trials
April frost damage	5			0.77–0.78		Nielsen and Roulund (1996)	Two clonal field trials
Autumn colouration	5			0.79–0.80		Nielsen and Roulund (1996)	Two clonal field trials
Leader break	5			0.39–0.46		Nielsen and Roulund (1996)	Two clonal field trials
Frost damage	4			0.92	0.45	Mboyi and Lee (1999)	Clonal/full-sub progeny
Height	1–11		0.14–0.38		0.43–0.61	Lee et al. (2002a)	Increase with age, one progeny test
	1		0.30			Samuel and Johnstone (1997)	
	3		0.14			Samuel and Johnstone (1997)	
	6		0.27			Samuel and Johnstone (1997)	
	0–10				0.91	Gill (1987)	One progeny trial series
	10				0.71	Gill (1987)	One progeny trial series
	4			0.93	0.88	Mboyi and Lee (1999)	Clonal/full-sub progeny
	5			0.68–0.77		Nielsen and Roulund (1996)	Across four sites
	9	0.36				Costa e Silva et al. (1998)	
	10	0.08–0.31				Hansen and Roulund (1997)	Four clonal field trials
	2–14			0.53–0.84		Jensen et al. (1997)	Three progeny field trials

(continued)

Table 4.7 (continued)

Trait	Age	Broad sense heritability (H^2)	Narrow sense heritability (h^2)	H^2 (clone mean)	h^2 (family mean)	Reference	Notes
Diameter	9	0.18				Costa e Silva et al. (1998)	
	10–23		0.19–0.43		0.56–0.59	Lee et al. (2002a)	Decrease with age
	21				0.53	Lee et al. (2007)	Grafted-ramet clone-mean heritability
	15				0.70	Lee (2001)	Many trials across 11 years
	10				0.71	Gill (1987)	One progeny trial series
	10	0.08–0.24				Hansen and Roulund (1997)	Four clonal field trials
	15	0.19				Hansen and Roulund (1998a, b)	Two progeny field trials
Volume	15				0.75	Gill (1987)	One progeny trial series
	21	0.65–0.87				Jensen et al. (1997)	Three progeny field trials
	9	0.21				Costa e Silva et al. (1998)	
Stem straightness (score)	21	0.68–0.86				Jensen et al. (1997)	Three progeny field trials
	9	0.40				Costa e Silva et al. (1998)	
	10	0.37				Hansen and Roulund (1997)	Four clonal field trials
	15				0.70	Lee (2001)	Many trials across 11 years
	14				0.45–0.67	Jensen et al. (1997)	Three progeny field trials

Lignin content	9	0.42		Costa e Silva et al. (1998)	
Wood density	6–9		0.96	Lee et al. (2002b)	One large progeny field trial
	8–22		0.79	Lee et al. (2002b)	One large progeny field trial
Pilodyn	20		0.73	Kennedy (2009)	One progeny trial
	10	0.32		Hansen and Roulund (1997)	One progeny field trial
	14		0.74–0.81	Jensen et al. (1996)	One progeny field trial
	15		0.80	Lee (2001)	Many trials across 11 years
Spiral grain (degrees)	Ring 6–8	0.36–0.54		Hansen and Roulund (1997)	Four clonal field trials
	Ring 10	0.63–0.78		Hansen and Roulund (1998a, b)	Two progeny field trials
Acoustic velocity	20		0.66	Kennedy (2009)	One progeny trial
Micro fibril angle	20		0.75	Kennedy (2009)	One progeny trial
Modulus of elasticity	20		0.47	Kennedy (2009)	One progeny trial
Modulus of rupture	20		0.62	Kennedy (2009)	One progeny trial
			0.69	Kennedy (2009)	One progeny trial
Green spruce aphid	22		0.72	Jensen et al. (1997)	One progeny field trial

Table 4.8 Examples of age-age and between-trait genetic correlations from a wide range of Sitka spruce progeny and clonal trials across Europe

Trait	Age	Trait	Age	Genetic correlation	Reference	Notes
Height	2–11	Diameter	23	0.28–0.83	Lee et al. (2002a)	Results from one progeny field trial
Height	3	Diameter	23	0.62		
Height	8	Diameter	23	0.77		
Height	11	Diameter	23	0.83		
Diameter	10	Diameter	23	0.90		
Wood density	Ring 6–9	Wood density	Ring 8–22	0.95	Lee (2001) Nielsen and Rolund (1996)	Many trials across 11 years Clone mean correlation Results from two field trials
Diameter	16	Wood density	Ring 8–22	–0.77		
Diameter	15	Pilodyn	15	–0.66		
Diameter	15	Stem straightness	15	0.04		
Pilodyn	15	Stem straightness	15	0.00		
Height	Nursery	Height	8	1		
		Flushing	8	–0.01 and 0.01		
		Autumn colouration	8	–0.06 and –0.12		
		Leader breaks	8	–0.06 and 0.01		
		Mortality	8	–0.10 and 0.02		
Height	5	April frost damage	8	0.14 and –0.12		
		Flushing	8	–0.05 and 0.03		
		Autumn colouration	8	–0.21 and –0.33		
		Leader breaks	8	–0.42 and –0.49		
		Mortality	8	–0.15 and –0.31		
Flushing	5	April frost damage	8	0.14 and 0.26		
		Autumn colouration	8	0.02 and –0.14		
		Leader breaks	8	0.18 and 0.17		
		Mortality	8	0.17 and 0.01		
		April frost damage	8	–0.33 and –0.37		
Leader breaks	5	Mortality	8	0.17 and 0.21		
		April frost damage	8	–0.31 and –0.14		
Mortality	5	April frost damage	8	–0.10 and –0.19		

Height	9	Diameter	9	0.62	Costa e Silva et al. (1998)	Results from one clonal field trial
	9	Volume	9	0.84		
	9	Pilodyn	9	0.24		
	9	Lignin	9	0.34		
	9	Stem straightness	9	0.16		
Diameter	9	Volume	9	0.96		
	9	Pilodyn	9	0.55		
	9	Lignin	9	0.47		
	9	Stem straightness	9	0.04		
Volume	9	Pilodyn	9	0.48		
	9	Lignin	9	0.42		
	9	Stem straightness	9	0.05		
Pilodyn	9	Lignin	9	0.15		
	9	Stem straightness	9	0.12		
Lignin	9	Stem straightness	9	-0.34		
Height	10	Diameter	13	0.68-0.86	Hansen and Roulund (1997)	Results from four clonal field trials
	10	Height	13	0.22		
Pilodyn	10	Diameter	13	0.53		
Diameter	10	Diameter	14	1.00	Hansen and Roulund (1998a, b)	Results from two progeny tests
		Spiral grain	10	-0.60		
Diameter	14	Spiral grain	10	-0.61		
		Stem straightness	14	0.08		
		Pilodyn	14	0.33		
Height	2	Height	14	0.53-0.85	Jensen et al. (1997)	Results from three progeny field trials
Height	14	Stem straightness	14	0.51-0.58		

(continued)

Table 4.8 (continued)

Trait	Age	Trait	Age	Genetic correlation	Reference	Notes
Grain angle	20	Acoustic velocity	20	-0.18	Kennedy (2009)	One progeny trial
Grain angle	20	Modulus of rupture	20	-0.05		
Grain angle	20	Modulus of elasticity	20	-0.14		
Grain angle	20	Microfibril angle	20	-0.50		
Grain angle	20	Wood density	20	-0.03		
Acoustic velocity	20	Modulus of rupture	20	0.49		
Acoustic velocity	20	Modulus of elasticity	20	0.81		
Acoustic velocity	20	Micro fibril angle	20	-0.83		
Acoustic velocity	20	Wood density	20	0.29		
Modulus of rupture	20	Modulus of elasticity	20	0.94		
Modulus of rupture	20	Micro fibril angle	20	-0.62		
Modulus of rupture	20	Wood density	20	1.04		
Modulus of elasticity	20	Micro fibril angle	20	-0.79		
Modulus of elasticity	20	Wood density	20	0.86		
Micro fibril angle	20	Wood density	20	-0.29		

Spiral grain: The angle of tracheids usually increases to the left and reaches a maximum in ring 5–10 after which it starts to decrease (Brazier 1967). The degree of spiral grain in rings 6, 8 and 10 is highly inherited with broad sense heritabilities and narrow sense heritabilities ranging from 0.36 to 0.78. The mean inclination in rings 6–10 is from 3.8° to 5.3° and the phenotypic standard deviation from 1.6° to 2.0° (Hansen and Roulund 1997, 1998a, b).

Other wood quality characteristics: There has been limited investigation on other wood quality traits. Work by Kennedy (2009) investigated approx. 30 open-pollinated 20-year old families growing on one site in Scotland suggests moderate to high family heritability for Modulus of Elasticity(MOE), Modulus of Rupture (MOR), Micro Fibril Length (MFA) and acoustic velocity.

Green spruce aphid: The green spruce aphid (*Elatobium abietinum* Walker) may occasionally attack Sitka spruce severely. The aphids feed on older needles and in extreme cases can cause total defoliation except of the current year needles (Jensen et al. 1997). Significant family differences, measured as needle loss, have been documented with a family heritability of 0.72 (Jensen et al. 1997). Additionally, needle loss in offspring from trees selected for low needle loss was indeed lower compared to offspring from a random reference stand.

Lignin content: The broad sense heritability for lignin content at DBH was 0.42 in a 9-year-old clonal field tests. The phenotypic standard deviation was 0.97 % and average lignin content 26.6 % (Costa e Silva 1996). Lignin content was moderately genetically correlated volume (0.42; Costa e Silva et al. 1999).

Stem straightness: Narrow and broad sense heritability for stem straightness in Sitka spruce scored on a scale from 1 to 9 is moderate – about 0.40 (Nielsen 1994). The phenotypic standard deviation was 1.1 and 1.3 in clonal tests evaluated by Costa e Silva et al. (1998) and Hansen and Roulund (1997). Lee (2001) and Lee and Connolly (2010) found family heritability of 0.70 following 1–6 scale assessment. Stem straightness is not genetically correlated with growth (Costa e Silva et al. 1998; Hansen and Roulund 1997; Lee 2001).

4.5.2 Age-Age Genetic Correlations and Selection Ages

Growth Rate: Studies of age-age correlations for growth in Sitka spruce are few, but genetic correlations seem generally high (above 0.60) between early height and diameter measurements (age 6 and more) and diameter at ages between 14 and 23 (Lee et al. 2002a; Jensen et al. 1996). Lee et al. (2002a) found as a consequence of the high age-age correlations that the optimal indirect selection for diameter age 23 was to select the best families (or mother plus tree) at age 5 for height, but to delay this to 9-year height when selecting the best individual within the best family.

Wood Density: Genetic correlations of wood density in ring 19–22 with groups of samples including three consecutive rings were all above 0.95 (Lee et al. 2002b).

The optimal age for selection estimated as gain per year (genetic gain per generation over generation interval) was as early as ring 6–9 due to the high genetic correlations between years (Lee et al. 2002b).

4.5.3 Genetic Correlations Between Traits

Growth rate with Wood density: The main challenge in the breeding of Sitka spruce is the negative correlation between wood density and growth rate. In British studies this relationship ranged from -0.64 to -0.80 depending on ring groups and ring numbers (Lee et al. 2002b). Cameron et al. (2005) found that wood density was lower for three fast growing 24-year-old progenies compared to three slow growing progenies, but the difference was not significant. Costa e Silva et al. (1994) also found that fast growing Sitka spruce clones retaining a high wood density did exist, demonstration a case for precise selection and mass-multiplication through clonal forestry.

Stem straightness with Growth rate and Wood Density. Stem straightness seems to be relatively independent of growth rate and stem straightness (Lee 2001; Jensen et al. 1996; Hansen and Roulund 1997; Lee and Connolly 2010). Some consider the relationship between stem straightness and growth may depend to a high degree on April frost damages and leader breaks (Jensen et al. 1996; Nielsen and Roulund 1996).

Spiral grain with Growth rate: Spiral grain from rings 6 to 10 seems reasonably independent of growth (Hansen and Roulund 1997, 1998a), but it is still uncertain if spiral grain in later rings will retain this relationship.

Relationships between other wood quality traits: Acoustic velocity is a good indication of MFA and MOE but not wood density; spiral grain and MOR are relatively independently correlated; MOR and wood density are highly correlated (Kennedy 2009).

4.5.4 Genotype-Environmental Interaction

Generally, genotype by environmental interactions ($G \times E$) are reported to be low and of minor importance in the countries that use, or have used, Sitka spruce to a larger extent (Ireland, Great Britain and Denmark), provided that trees of different origins are not compared across sites in error. Within origin $G \times E$ appears low. In an evaluation of two 5-year-old clonal field trial series in Denmark the genetic correlations across sites ranged from 0.55 to 0.78 for height, and from 0.50 to 0.71 for diameter; $G \times E$ was of minor importance (Nielsen and Roulund 1996). Similarly, genetic correlations across sites ranged between 0.56 for height and 0.85 for diameter in a 10-year-old clonal field trial series (Hansen and Roulund 1997). However,

Jensen et al. (1996) found a correlation across sites of just 0.28, but this study included a small sample of only 15 open pollinated families. Johnstone and Samuel (1978) found that first fears of high $G \times E$ were ill-founded following analysis of data collected in some of the first open-pollinated progeny tests. They concluded that the number of test sites could be reduced from eight to three across Britain which typically became one each in the main Sitka spruce growing areas of Britain (North Scotland, South Scotland/Northern England, and Wales).

4.6 Wood Quality

Sitka spruce is a white-wood species and therefore attractive to the paper making industry although most growers are hoping to satisfy the solid-wood construction market. Improvement of growth rate, stem straightness and branching quality are relatively straight-forward to achieve due to neutral or positive genetic correlations, but the addition of wood density and other wood-related characters becomes a challenge for breeders due to the often negative genetic correlations with growth rate.

The density of Sitka spruce is relatively low (390 kg m^{-3}) compared to other conifer species such as Scots pine (*Pinus sylvestris*; 510 kg m^{-3}) Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco; 530 kg m^{-3}) or European larch (*Larix decidua* Mill.; 540 kg m^{-3} ; Harding 1988). Absolute wood density should not be allowed to fall further in Sitka spruce. Both silviculture, and selection and breeding will influence final timber quality and this has been fully reviewed by MacDonald and Hubert (2002). Moore et al. (2009a) found that wood strength (MOR) was not a particular problem at standard spacing (around $2 \times 2 \text{ m}$) but that wood stiffness (MOE) was a major problem. If breeders want Sitka spruce timber to significantly penetrate the construction market, then an improvement in MOE is required. Further work by Moore et al. (2009b) concluded that very wide spacing (less than 900 trees per hectare or $3.3 \times 3.3 \text{ m}$) is not recommended even if the goal is to produce the lowest quality of construction timbers (C16; CEN 2003).

4.7 Forest Reproductive Material Deployment and Genetic Gains

Table 4.4 gives an indication of the sources of improved Sitka spruce across Europe. There are 8 seed orchards in Great Britain, 4 in Denmark, 3 in Norway and 1 in France. Ireland has only recently chosen to establish seed orchards and up to now has depended on deploying improved material through vegetative propagation following controlled pollination, which is also a technique used by Great Britain. Table 4.6 gives an indication of sources of the planting stock within each country. There is barely a need to return to the Pacific North West with all countries sourcing material from their own improved or landrace stocks.

Predicted gains from production populations of the different Sitka spruce breeding programs largely reflects the breeding objectives and the resources made available to carry out the programme which are depended on the importance of the species to the respective forest resource. Despite the generally unfavourable negative correlation between wood density and growth rate, it is still possible to improve growth while retaining wood density providing sufficient plus trees are initially selected (2,000 or so) from which to re-select based on results from subsequent genetic evaluation trials. Predicted gains are summarised in Table 4.4 with a more detailed analysis presented in Table 4.9.

The predicted genetic gains are naturally dependent on a reference point which in comparative trials in Britain and Ireland is unimproved material from QCI and Washington State (respectively). The experience in Denmark is that landraces are much better adapted compared to direct imports resulting in higher survival rates and growth (Nielsen 1994).

4.7.1 Final Rotation Gains

The end of rotation volume gain from planting improved Sitka spruce stock in Great Britain has been estimated by Lee and Matthews (2004) at between 21 and 29 % relative to unimproved QCI material. This is a significant volume gain implying that every hectare planted with improved material will yield around 25 % more volume of timber at rotation age (35–50 years old). Similar figures are presented for volume gain from one of the Danish orchards of Washington origin.

Further studies to investigate quality traits by Mochan et al. (2008) indicated that substantial improvements in straightness are a further benefit from the UK breeding programme. One of the earliest progeny trials (planted 1967) testing just a few plus trees but in large plots, was felled at 37-years-old. Various characteristics relating to quality and growth rate were assessed in the forest and sawmill as well as the volume of high quality (green) sawlogs, and sawn timber meeting the strength classes C16 and C24 (CEN 2003). Three improved lots with respectively the highest wood density, fastest growth rate and best stem form were compared to the QCI control. Results at both the individual tree and per hectare level showed increased sawn timber volumes from improved planting stock without deterioration in construction grade strength requirements. In the best progeny, increases of up to 130 % in both green (high-quality) sawlog and sawn timber volumes per hectare were predicted with equivalent mechanical properties to the QCI stock. Further work by Lee and Watt (2012) suggests that the likely increase in quality logs from seed orchard material will be 20 % and that the gains from full-sib families available through vegetative propagation would be closer to 40 %.

Table 4.9 Examples of predicted genetic gain from different Sitka spruce breeding programmes across Europe

Material from:						
Country	Year	Trait	Age	Seed orchard (%)	Vegetative propagation (half sib family mixes) (%)	Vegetative propagation (full sib families) (%)
Great Britain	2010	Diameter	15	15–20	20	20–30
		Stem straightness	15	10–15	20	15–30
		Branching score	15			10–15
		Wood density	15	–10 to 0	0	0–10
		Rotation sawlog volume	Rotation age	Approx. 40	Approx. 50	Approx. 60
Ireland	2010	Rotation volume	Rotation age	Approx. 20	Approx. 30	Approx. 30
		Height		15–20		
Denmark	2010	Stem form		7		
		Diameter	15	7		
		Stem straightness	15	12		
		Volume	18	30		
		Wood density ^b	18	0		
		Leader breaks	18	–7		
		Stem straightness	18	4		
		Forks	18	–3		
		Stem straightness	10	11		
		Diameter	10	5		
		Wood density ^b	10	0		
		Flushing score	5	–12		
Queen Charlotte import ^a		Stem straightness	10	14		
Queen Charlotte import ^a						
Unimproved stock						
Unimproved Danish landrace						
Unimproved Danish landrace						
Unimproved Danish landrace						
Unimproved Danish landrace						

(continued)

Table 4.9 (continued)

Material from:						
Country	Year	Trait	Age	Seed orchard (%)	Vegetative propagation (half sib family mixes) (%)	Vegetative propagation (full sib families) (%)
		Stem straightness	10	11 (5)		
		Spiral grain	6–8	–8 (–3)		
		Diameter	10	5 (37)		
		Wood density ^b	10	0		
		Height	Rotation age	–5		
		Diameter	Rotation age	–7		
		Green spruce aphid resistance (needle loss)		–50		
		Stem straightness		1		
		Survival		–1		
		Forking		2		
		Leader breaks		–8		
		Wood density ^b		1		
						Clone mean ^c or Queen Charlotte Island import in bracket
						Unimproved Danish landrace

^aWork in hand. Approx. figures only quoted here. Based on data from Mochan et al. (2008) and Lee and Matthews (2004). Contact steve.lee@forestry.gsi.gov.uk for up to date figures

^bWood density measured indirectly using the pilodyn instrument

^cClones from Danish landrace of Washington origin



Fig. 4.18 Harvesting SS cuttings from a hedge orchard in Ireland (Source: Coillte, Ireland)

4.7.2 Seed Orchards or Vegetative Propagation?

Sitka spruce lends itself to a traditional vegetative propagation programme (Mason and Gill 1986). A single seed can yield over 1,000 rooted cuttings for deployment if the nursery managers do their job well. The extra handling costs of VP material does tend to increase its cost relative to seed orchard material. In Great Britain, improved material is now available from both tested clonal seed orchards (SO) and vegetative propagation (VP) of tested full-sibling families. Similarly VP material is available in Ireland and SO material is available from Denmark (Fig. 4.18).

Currently, VP material costs the forest manager around twice the price per thousand plants as SO material and yet predicted gains for growth traits are predicted as similar

in Britain. The extra planting cost is only justified if trees are planted on more fertile sites which are also likely to remain standing until late or normal rotation age (YC16 or more; 40 years old or more) This is necessary to realise the size of trees which will allow the extra sawlogs predicted from the VP stock to actually be produced. Further improvements in uniformity of VP full-sib stock relative to SO material suggest more utilisable timber standing on each hectare of ground. VP stock is not therefore appropriate for all planting sites with existing cost differentials. Less fertile sites with expected shortened rotations due to wind should be planted with seedling improved stock from clonal seed orchards.

An alternative approach used successfully in Ireland to reduce the higher cost of VP stock has been to plant a mixture of improved VP stock with unimproved seedling material. An economic analysis (Philips and Thompson 2010) has shown that the additional cost of planting 50 % of the trees as VP planting stock is more than recovered by the increased wood volume at final harvest.

4.7.3 *Clonal Forestry*

Preliminary work pioneered in Denmark (Roulund 1978, 1981) showed the benefits of using clonally propagated Sitka spruce including the selection for clones with superior growth rates (Nielsen and Roulund 1996), nutrient use efficiency (Sheppard and Cannell 1985) and those that combine high basic density with good growth rates (Costa e Silva et al. 1994). Similar results demonstrating the benefits of clonal forestry have also been found in Britain (Mboyi and Lee 1999).

Clonal forestry is not yet being practiced on anything other than a research scale. The main limitation is that although cuttings propagation is common, only around 1,000 rooted cuttings can be cropped from a donor plant or hedge before ageing problems result in reduced rooting success and plagiotrophic growth (Mason and Gill 1986; Mason et al. 2002). This number is too small for commercial deployment of a tested clone, but also field trial results will not be available within the time scale in which it can be easily propagated. Deployment of tested clones will only be successful once protocols of SE and cryopreservation can be made to work reliably and cost effectively. Once perfected, these techniques could be used to generate thousands of copies of tested clones. Work is still progressing to perfect working, commercial protocols particularly for successful cryopreservation (Kristensen et al. 1994; Find et al. 1998; Lee et al. 2004; Thompson and Harrington 2005; John et al. 2007) (Fig. 4.19).

Once SE/cryo techniques are perfected it remains to be seen if the practice can be made to work on a commercial scale. An economic exercise will be required to investigate under what circumstances of predicted gain and extra cost of planting stock, relative to cuttings or seedlings, clonal forestry could be considered a viable option. The technology is perhaps suitable for automation with robots and this could reduce unit price considerably as has already been demonstrated for Nordmann fir and Sitka spruce (Find and Krogstrup 2008).

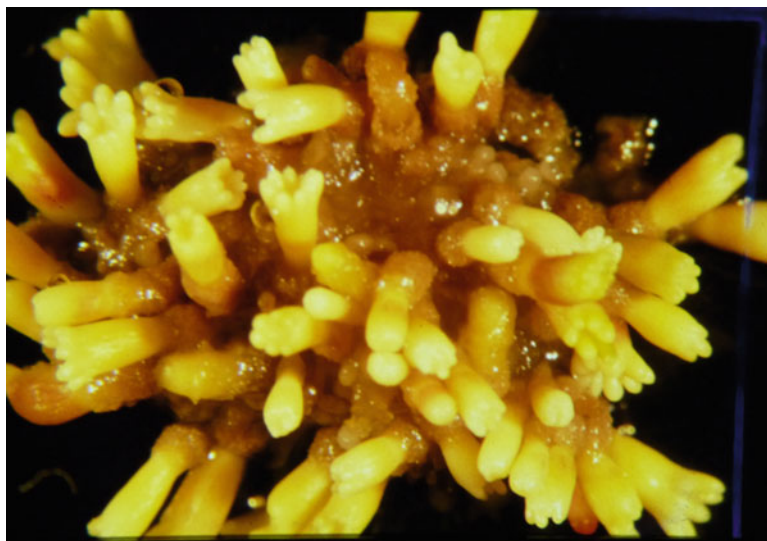


Fig. 4.19 Sitka spruce somatic embryos (Source: Coillte Teoranta, Ireland)

4.7.4 Flower Engineering to Improve FRM Quantities

The long juvenile phase and irregular flowering of mature Sitka spruce trees and grafted scions have often been a reason for delays in the breeding progress and production of improved seed. Also there is known to be huge variation in flowering potential between individuals. This is the reason Ireland chose to ignore seed orchards and concentrate on VP as a source of deployment of improved material.

Research carried out in Great Britain found that flowering can be consistently induced in potted grafts under polythene by stem injections of a mixture of gibberellic acids four and seven ($GA_{4/7}$) in combination with drought and high temperature (Philipson 1983, 1985). The induction of flowering in field grown plants does not give such predictable results due to the less controllable conditions. However, $GA_{4/7}$ injection is routinely used in clone banks and has been found to boost flower numbers in moderate or good flowering years. There is no research into flower-engineering currently being carried out on Sitka spruce in Europe.

4.8 Knowledge Gaps and Research Needs

The main areas requiring further research are:

1. Advancing the flowering age of juvenile plants;
2. Fully operational protocols for clonal forestry technologies;

3. Economic models of the complete wood chain enabling assessment of the value of breeding for different characteristics;
4. Learning more about what controls the strength of Sitka spruce timber, how these characteristics interact and possible future novel uses for Sitka spruce timber;
5. Very early indirect selection for important traits such as growth rate and wood quality. This would include DNA-marker studies leading to Marker Assisted BLUP (Best Linear Unbiased Predictor) evaluations as are currently being developed in dairy cattle (Hayes et al. 2009).

No research work has been carried out into reducing the juvenile phase and advancing the age at which flowering occurs in selected genotypes. This remains a bottleneck in the breeding process as it is often 15–20-years or more before flowering occurs in Sitka spruce. Possible areas for development would be application of the techniques developed by Philipson on juvenile individuals and top-grafting of juvenile scions into the upper crown of unrelated mature grafts as described by McKeand and Raley (2000) in Loblolly pine (*Pinus taeda*).

The research needs listed above are all currently under investigation by one or more of the European countries interested in the commercial planting of Sitka spruce, and these skills can often be easily transferred from a different species already being grown in Europe.

4.9 European-Wide Breeding Perspectives

Despite the relatively limited interest in Sitka spruce as a commercial species across Europe, it is of importance to countries such Great Britain, Ireland and Denmark which have well developed improvement programmes. There is scope for more co-operation between these countries and those that have an interest in the species but no resources for breeding. There is increasing interest in the species in Sweden and possibly France as the climate changes but interest in Germany and Norway is unlikely to increase.

The main origins of Sitka spruce planted across Europe are Washington, which is being actively developed by Ireland and in the past by Denmark, and QCI which is being aggressively pursued by Great Britain. If there is a future increase in demand from other countries for improved material of either of these origins, it can be made available. New countries planting increasingly more Sitka spruce should consider sourcing trees from established improvement programmes (of suitable origin) available elsewhere in Europe before commencing their own programme.

New climatic conditions may lead to further pan-European co-operation, particularly if existing Sitka spruce users look to more southerly origins. Such a move would not usually be made without evidence from replicated, realised gain trials comparing, for example, the highly bred QCI-origin material against less intensively bred Washington or Oregon sources on suitable sites. Existing EU contracts such as TreeBreedEx have encouraged Sitka breeders across the Atlantic fringe of Europe to network and share seed, pollen, genotypes, and to exchange and test their

respective improved material. It could be hypothesized that the QCI – based programme in Great Britain could make way for a more Washington-based material if the climate warms and the occurrence of autumnal frosts is sufficiently delayed. However, such a switch would not be based on growth rate alone and would have to consider other genetic gains made to date in the advanced-bred QCI-based stock for characteristics such as stem, branch, and wood quality traits i.e. there would have to be a comparison their respective economic value to the end user.

Sharing need not be restricted to breeding material. Knowledge also needs to be shared in an effort to reduce the cost of breeding programmes and increase efficiencies. Such co-operation could be limited to periodic meetings for an exchange of information and ideas, but could also expand to include the exchange of material for comparative trials. In addition there could be some benefits from combined meetings with Norway spruce breeders because of the similarities between the species, especially in the area of clonal forestry technologies.

While most national programmes have developed to meet national needs, sometimes the national needs have limited the focus of the improvement programme. Nevertheless good co-operation exists between Great Britain, Ireland and Denmark in the exchange of information and technology. Examples include sharing knowledge of SE and cryogenic storage between Great Britain and Ireland, and the supply of improved material to Ireland from Danish seed orchards, and of seed orchard and VP stock from Great Britain to Sweden.

These informal arrangements could be built upon and expanded to other countries who may be interested in the species. Further efficiencies might be to prevent duplication of efforts by having one country develop each of the following:

1. DNA-marker techniques (e.g. Great Britain);
2. Clonal forestry techniques (Ireland, GB or Denmark);
3. BLUP evaluation techniques (e.g. Sweden or France);
4. Wood quality knowledge (e.g. GB or France).

Sitka spruce is likely to remain a key but localized European species for the future. It is clearly already an important species in Great Britain and Ireland and it remains to be seen how interest develops in other countries, particularly Sweden as the climate warms. As resources for breeding decline at a national level it makes sense to combine resources across countries or concentrate a particular expertise in one country for the benefit of all of Europe.

References

- Bauger E (1978) Growth of some Sitka spruce provenances in older plantations in West Norway and North Norway. Rep For Res Inst West Nor 54(14/7):365–454 [English summary]
- Brazier JD (1967) Timber improvement I: a study of variation in wood characteristics in young Sitka spruce. Forestry 40:117–138
- Cameron A, Lee SJ, Livingston AK, Petty JA (2005) Influence of selective breeding on the development of juvenile wood in Sitka spruce. Can J For Res 35(12):2951–2960

- Cannell MGR, Sheppard LJ, Smith RI, Murray MB (1985) Autumn frost damage on young *Picea sitchensis* 2. Shoot frost hardening, and the probability of frost damage in Scotland. *Forestry* 58:145–166
- CEN (2003) Structural timber – strength classes. EN 338:2003. European Committee for Standardization, Brussels
- Costa e Silva J (1996) Clonal variation in wood quality, growth and growth rhythm in young Sitka spruce (*Picea sitchensis* (Bong.) Carr.): indirect assessment of wood density and lignin amount, estimation of quantitative genetic parameters, and index selection for improved pulpwood. Ph.D. thesis, Royal Veterinary- and Agricultural University, Frederiksberg, 157pp
- Costa e Silva J, Nielsen UB, Roulund H (1994) Sitka spruce clonal performance with special reference to basic density. *Silvae Genetica* 43:82–91
- Costa e Silva J, Wellendorf H, Pereira H (1998) Clonal variation in wood quality and growth in young Sitka spruce (*Picea sitchensis* (Bong.) Carr.): estimation of quantitative genetic parameters and index selection for improved pulpwood. *Silvae Genetica* 47:20–33
- Costa e Silva J, Nielsen BH, Rodrigues J, Pereira H, Wellendorf H (1999) Rapid determination of the lignin content in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) wood by Fourier transform infrared spectrometry. *Holzforschung* 53:597–602
- Find J, Krogstrup P (2008) Integration of biotechnology, robot technology and visualisation technology for development of methods for automated mass production of elite trees. In: Working papers of the Finnish Forest Research Institute 114 “Vegetative propagation of conifers for enhancing landscaping and tree breeding”. Proceedings of the Nordic meeting held 10–11 Sept 2008, Punkaharju
- Find JI, Kristensen MMH, Nørgård J, Krogstrup P (1998) Effect of culture period and cell density on regrowth following cryopreservation of embryogenic suspension cultures of Norway spruce and Sitka spruce. *Plant Cell Tissue Organ Cult* 53:27–33
- Fletcher AM, Faulkner R (1972) A plan for the improvement of Sitka spruce by breeding and selection Forestry Commission Research and Development Paper, 85, London
- Forestry Commission (2008) Forestry statistics. 2008 – woodland areas and planting. Forestry Commission, Edinburgh. <http://www.forestry.gov.uk/forestry/infid-7aqdgc>
- Forestry Commission (2010) Nursery survey 2010. Forestry statistics press release. Forestry Commission, Edinburgh. <http://www.forestry.gov.uk/forestry/AHEN-5EBDYX>
- Geburek TH, Krusche D (1985) Wachstum von Hybriden zwischen *Picea omorika* und *P. sitchensis* im Vergleich zu den Elternarten. *Allg Forst, u J -Ztg* 156:47–54
- Gill JGS (1987) Juvenile-mature correlations and trends in genetic variances in Sitka spruce in Britain. *Silvae Genet* 36(5–6):189–194
- Grieser J, Gommers R, Bernardi M (2006) New LocClim – the local climate estimator of FAO. *Geogr Res Abstr* 8:08305
- Hansen JK, Roulund H (1997) Genetic parameters for spiral grain, stem form, pilodyn and growth in 13 years old clones of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Silvae Genet* 46:107–113
- Hansen JK, Roulund H (1998a) Spiral grain in a clonal trial with Sitka spruce. *Can J For Res* 28:911–919
- Hansen JK, Roulund H (1998b) Genetic parameters for spiral grain in two 18-year-old progeny trials with Sitka spruce in Denmark. *Can J For Res* 28:920–931
- Harding T (1988) British softwoods: properties and uses. Forestry Commission Bulletin 77, Forestry Commission, Edinburgh, p 41
- Hayes BJ, Bowman PJ, Chamberlain AJ, Goddard ME (2009) Genomic selection in dairy cattle: progress and challenges. *J Dairy Sci* 92:433–443
- Hoffman D, Kleinschmit J (1979) A utilization program for spruce provenance and species hybrids. In: Proceedings of the IUFRO joint meeting of working parties on Norway spruce provenances and Norway spruce breeding, Bucharest, 1979, pp 216–236
- Jensen JS, Kjaer ED, Roulund H (1996) A progeny trial in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in Denmark. Age-age correlation and between traits and trials correlation. *Silvae Genetica* 45:85–90

- Jensen JS, Harding S, Roulund H (1997) Resistance to the green spruce aphid (*Elatobium abietinum* Walker) in progenies of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). For Ecol Manage 97(3):207–214
- John A, Gale S, Benson E (2007) Tissue culture and cryopreservation of Sitka. For Br Timber 36(7):53–58
- Johnstone RCB, Samuel CJA (1978) The interactions between genotype and site: its influence on tree selection programmes in Britain. Forestry Commission research and development paper 122, 18 pp, Presented at the eight world forestry congress, Jakarta
- Joyce PM, O'Carroll N (2002) Sitka spruce in Ireland. COFORD, Dublin, 201p
- Karlsson BL (1995) Breeding of Sitka spruce (*Picea sitchensis*) and Douglas fir (*Pseudotsuga menziesii*) in south Sweden. Buvisindi Icel Agric Sci 9:119–122
- Karlsson B (2007) Sitka- och Douglasgran – alternativ för ett nytt klimat, Resultat nr 17. Skogforsk, Uppsala (in Swedish)
- Kennedy SG (2009) Improving the wood strength of Sitka spruce (*Picea Sitchensis*) through selective breeding. Ph.D. thesis, Aberdeen University, Aberdeen, 89pp
- King JN, Alfaro RI, Cartwright C (2004) Genetic resistance of Sitka spruce (*Picea sitchensis*) populations to the white pine weevil (*Pissodes strobi*): distribution of resistance. Forestry 77:269–278
- Kleinschmit J (1974) A programme for large-scale cutting propagation of Norway spruce. N Z J For Sci 42(2):359–366
- Kranenborg KG, de Vries SMG (2003) International provenance research of Sitka spruce in the Netherlands (in Dutch with English summary), Alterra-rapport 846. Alterra, Research Instituut voor de Groene Ruimte, Wageningen, 31pp
- Kristensen MMH, Find JI, Floto F, Møller JD, Nørgaard JV, Krogstrup P (1994) The origin and development of somatic embryos following cryopreservation of an embryogenic suspension culture of *Picea sitchensis*. Protoplasma 182:65–70
- Lee SJ (2001) Selection of parents for the Sitka spruce breeding population in Britain and the strategy for the next breeding cycle. Forestry 74(2):129–143
- Lee SJ (2006) It's a family affair. For Br Timber 35(12):14–16
- Lee SJ, Connolly T (2010) Finalising the selection of parents for the Sitka spruce (*Picea sitchensis* (Bong.) Carr) breeding population in Britain using mixed model analysis. Forestry 83(4):423–431
- Lee SJ, Matthews R (2004) An indication of the likely volume gains from improved planting Sitka spruce stock. Forestry Commission Information Note 55, Forestry Commission, Edinburgh
- Lee SJ, Woolliams J, Samuel CJA, Malcolm DC (2002a) A study of population variation and inheritance in Sitka spruce II. Age trends in genetic parameters for vigour traits and optimum selection ages. Silvae Genetica 51(2–3):55–65
- Lee SJ, Woolliams J, Samuel CJA, Malcolm DC (2002b) A study of population variation and inheritance in Sitka spruce. III Age trends in genetic parameters and optimum selection ages for wood density, and genetic correlations with vigour traits. Silvae Genetica 51(4):143–151
- Lee SJ, Cottrell J, John A (2004) Advances in biotechnology: powerful tools for tree breeding and genetic conservation. Forestry Commission Information Note 50, Forestry Commission, Edinburgh, p 5
- Lee SJ, A'Hara S, Cottrell J (2006) The use of DNA technology to advance the Sitka spruce breeding programme. In: Forest research annual report and accounts 2005–2006. Forestry Commission, Edinburgh
- Lee SJ, Watt G (2012) Improved Sitka spruce planting stock; seedlings from a clonal seed orchard or cuttings from full-sibling families? Scott For 66(2):18–25
- Lee SJ, Woolliams J, Samuel CJA, Malcolm DC (2007) A study of population variation and inheritance in Sitka spruce IV. Correlated response in the progeny population based on selection in the parental population. Silvae Genetica 56(1):36–44
- MacDonald E, Hibert J (2002) A review of the effects of silviculture on timber quality of Sitka spruce. Forestry 75(2):107–138

- Mason WL, Gill JGS (1986) Vegetative propagation as a means of intensifying wood production in Britain. *Forestry* 59(2):155–183
- Mason WL, Menzies MJ, Biggin P (2002) A comparison of hedging and repeated cutting cycles for propagating clones of Sitka spruce. *Forestry* 73(2):149–162
- Mboyi WM, Lee SJ (1999) Incidence of autumn frost damage and lammas growth in a 4-year-old clonal trial of Sitka spruce (*Picea sitchensis*) in Britain. *Forestry* 72(2):135–146
- McKeand SE, Raley EM (2000) Interstock effects on strobilus initiation in top grafted loblolly pine. *For Genet* 7:179–182
- Mochan S, Lee S, Gardiner B (2008) Benefits of improved Sitka spruce: part 1. Volume and quality outturn. Forestry Commission Research Note No. 3, Edinburgh, 6pp
- Mochan S, Connolly T, Moore J (2009) Using acoustic tools in forestry and the wood supply chain. Forestry Commission Technical Note 18, Edinburgh, 6pp
- Moore J, Achim A, Lyon A, Mochan S, Gardiner B (2009a) Effects of early re-spacing on the physical and mechanical properties of Sitka spruce structural timber. *For Ecol Manage* 258:1174–1180
- Moore JR, Mochan SJ, Bruchert F, Hapca AI, Ridley-Ellis DJ, Gardiner BA, Lee SJ (2009b) Effects of genetics on the wood properties of Sitka spruce growing in the UK: bending strength and stiffness of structural timber. *Forestry* 82(5):491–501
- Nielsen UB (1994) Genetisk variation i sitkagran (*Picea sitchensis* (Bong.) Carr.) i højdevækst, stammeform og frosthærdighed – vurderet ud fra danske proveniens-, afkoms- og klonforsøg [Genetic variation in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) regarding height growth, stem form and frost hardness at the provenance, progeny, and clonal level, based on Danish field trials]. Ph.D. thesis, The Royal Veterinary and Agricultural University, Forskningscentret for Skov- & Landskab, Forskningsserien Nr. 9, 332pp
- Nielsen UB, Roulund H (1996) Genetic variation in characters of importance for stand establishment in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Silvae Genetica* 45:197–204
- Nord-Larsen T, Johannsen VK, Jørgensen BB, Bastrup-Birk A (2008) Skove & Plantager, 2006 [Forest and plantations, in Danish]. Skov & Landskab, Københavns Universitet, Hørsholm, 185pp
- Øyen B-H (2005) Growth and yield in stands of Sitka spruce (*Picea sitchensis* Bong. Carr.) in Norway. Research paper from Skogforsk 4/2005, pp 1–46 [English summary]. <http://www.skogoglandskap.no/filearchive/r-2005-4.pdf>
- Peterson EB, Peterson NN, Weetman GF, Martin PJ (1997) Ecology and management of Sitka spruce emphasizing its natural range in British Columbia. UBC Press, Vancouver, 336
- Philips H, Thompson D (2010) Economic benefits and guidelines for planting improved Washington Sitka spruce. COFORD Connects Reproductive Material Note No. 17, COFORD, Dublin, 4 p
- Philipson JJ (1983) The role of gibberellin A4/7, heat and drought in the induction of flowering in Sitka spruce. *J Exp Bot* 34:291–302
- Philipson JJ (1985) The promotion of flowering in large field-grown Sitka spruce by girdling and stem injections of gibberellin A4/7. *Can J For Res* 15:166–170
- Roche L (1969) A genealogical study of the genus *Picea* in British Columbia. *New Phytol* 68:504–554
- Roche L, Fowler DP (1975) Genetics of Sitka spruce. Research Paper WO-26, US Department of Agriculture, Forest Service, US Government Printing Office, Washington, DC, 15pp
- Roulund H (1978) A comparison of seedling and clonal cuttings of Sitka spruce (*Picea sitchensis* (Bong.) Carr.). *Silvae Genetica* 27(3–4):104–108
- Roulund H (1981) Problems of clonal forestry in spruce and their influence on breeding strategy. *For Abstr* 42(10):457–471
- Roulund H (1990) Outline to a revision of the Sitka spruce breeding plan in Denmark. *For Tree Improve* 23:131–144
- Samuel CJA, Johnstone RCB (1997) A study of population variation and inheritance in Sitka spruce. I. Results of glasshouse, nursery and early forest progeny tests. *Silvae Genetica* 28(1):26–32

- Samuel CJA, Fletcher AM, Lines R (2007) Choices of Sitka spruce origins for use in British forests. For Comm Bull 127:, 112 pp
- Sheppard LJ, Cannell MGR (1985) Nutrient use efficiency of clones of *Picea sitchensis* and *Pinus contorta*. *Silvae Genetica* 34(4–5):126–132
- Thompson D (2007) Where should Washington and Oregon sources of Sitka spruce be planted in Ireland? COFORD Connects Reproductive material Note No. 11. COFORD, Dublin, 2p
- Thompson D, Harrington F (2005) Sitka spruce (*Picea sitchensis*). In: Jan SM, Gupta PK (eds) Protocol for somatic embryogenesis in woody plants. Springer, Dordrecht, pp 69–80
- Thompson DG, Pfeifer AR (1995) IUFRO Sitka spruce provenance trial – 19 year results. In: Evolution of breeding strategies for conifers from the Pacific Northwest, Joint meeting of IUFRO working parties S2.02, 05, 06, 12 and 14 (Douglas-fir, *Pinus contorta*, Sitka spruce and *Abies*), Limoges
- Thompson D, Lally M, Pfeifer A (2005) Washington, Oregon or Queen Charlotte Islands? Which is the best provenance of Sitka spruce (*Picea sitchensis*) for Ireland? *Ir For* 62(1–2):19–39
- Ying CC, McKnight LA (eds) (1993) Proceedings of the IUFRO international Sitka spruce provenance experiment. Ministry of Forests, Victoria